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Buteo polyosoma and *Buteo poecilochrous* are two distinct species

by Jose Cabot & Tjitte de Vries

The Red-backed Hawk *Buteo polyosoma* Quoy and Gaimard 1824 occurs from southwest Colombia south to the southern Andes, together with the Pampa region of Argentina, Patagonia, Tierra del Fuego and the Falkland and Juan Fernandez Islands. Southern birds migrate to the lowlands of northern and central Argentina, eastern Bolivia, Uruguay, Paraguay, the Mato Grosso and southern Brazil in winter (Schubart *et al.* 1965, Contreras *et al.* 1990, Fjeldså & Krabbe 1990, Cabot & Serrano 1988). Cabot (1988, 1991) reported the occurrence of wintering individuals in the Bolivian Altiplano. It occurs from sea-level to 4,500 m.

The Puna Hawk *Buteo poecilochrous* Gurney 1879 inhabits rocky regions and cliffs in rugged paramo and puna terrain, rocky Andean ridges and Altiplano from Colombia to northern Argentina and Chile. It is sedentary and occurs between 3,000 and 5,500 m (Lehmann 1945, Dorst 1954, Solís & Black 1985, Fjeldså & Krabbe 1990, Cabot 1988).

B. polyosoma and *B. poecilochrous* are considered to be closely related to one another, and to other hawks such as the White-tailed Hawk *B. albicaudatus*, Galapagos Hawk *B. galapagoensis* and Swainson's Hawk *B. swainsoni* (Brown & Amadon 1968, de Vries 1973, Voous & de Vries 1978). The separation of *B. poecilochrous* and *B. polyosoma* was based exclusively on external characteristics (Stresemann 1925, Chapman 1926, Hellmayr 1932, Vaurie 1962, de Vries 1973), although the small difference in size between the two taxa, their polymorphic plumages with some patterns virtually duplicated, and their partial range overlap has fuelled a long debate over their exact taxonomic identity. Nevertheless, most authors still recognise *B. polyosoma* and *B. poecilochrous* as two distinct species.

Farquhar (1998), on the other hand, concluded that *B. polyosoma* and *B. poecilochrous* are conspecific and should be regarded as one species, namely *Buteo polyosoma*. This author argued that the morphological differences are due to clinal and altitudinal variation in size and body mass, and also used plumage and voice characteristics to support his proposal.

In this study we demonstrate that *B. polyosoma* and *B. poecilochrous* are separate species, with different morphology and body size, on the basis of an analysis of the external measurements of skins and of live birds. The two phenotypes are identifiable in the hand by a range of body measurements. We also demonstrate that there is no inter-gradation or clinal gradient between the two entities; where the two taxa occur in the same altitudinal range in the high Central Andean region, morphological differences are maintained. Furthermore, Stresemann's key for separating the two species, based on the differences in the wing formula (the third outermost primary, P8, is constantly longer than fifth, P6, in *polyosoma*, the reverse being true in *poecilochrous*) is re-evaluated. We examine the effects of using wrongly identified, wrongly sexed or unsexed birds on taxonomic decisions regarding the two taxa. We re-analyse Farquhar's work, using his material and methods, and re-assess his results and conclusions. All this, together with ecological and behavioural factors, leads us to conclude that the original status of full species should be assigned to each of the two taxa, in accordance with the biological species concept.

Material & methods

We examined 118 skins of both taxa held at the Natural History Museum, Tring; Zoologisk Museum, Copenhagen; Museo Regionale di Science Naturali, Torino; Institut Royal des Sciences Naturelles de Belgique; Museum national D´Histoire naturelle, Paris; Estación Biológica de Doñana, Sevilla; and Museo Nacional de Ciencias Naturales, Madrid. Study skins of *polyosoma* were from Ecuador (1), Peru (13), Bolivia (17), Argentina (16), Chile (23), the Falkland Islands (2) and of unknown origin (2), while those of *poecilochrous* were from Ecuador (6), Peru (14), Bolivia (17), Argentina (1), Chile (3) and of unknown origin (3).

Controversial and undated skins were identified and sexed on the basis of the length of the secondaries, wing width, wing depth and the shape of the wing tips,

according to the range of values given by de Vries (1973) and Cabot (1991). Additionally, 16 live birds from Peru (11 *B. polyosoma* and 5 *B. poecilochrous*), in private zoos and hawking centres, were examined.

Measurements

Comparison of the two species was based on the following measurements (with an emphasis on those related to wing shape) of museum skins: mass obtained from data on label; culmen from cere; culmen from base, from the tip of the bill to the angle at the front of the skull; cranial width (post-orbital); length of the cubito-radius; tarsus; inner toe, middle toe, outer toe and hind toe; inner claw, middle claw, outer claw and hind claw (all measurements taken with a calliper to the nearest 0.01 mm). Wing length; length of emargination and notch of the five outermost primaries (P6, P7, P8, P9, P10), from the beginning of the feature to the tip; consecutive distances between the tips of the five outermost primaries (P9-P10, P8-P9, P7-P8, P6-P7) and the width of the free fingers of the three outermost primaries at the point where both emargination and notch start to coincide (Fig. 1). Wing length and feather lengths: alula, outermost primary (P10), the outermost and innermost secondaries were measured at their maximum length (straightened and flattened against a ruler to the nearest 0.5 mm). Tail and feathers were measured (nearest 1mm) from their base at skin insertion to their distal extreme.

The data taken from live birds were as follows: (a) body mass (g) using a digital balance; (b) gender determined by body measurement (de Vries 1973), and by the use of a molecular technique (Ellegren 1996) (all results coincided for all individuals); (c) wing-span (mm) using a measuring tape – two helpers held birds face up with
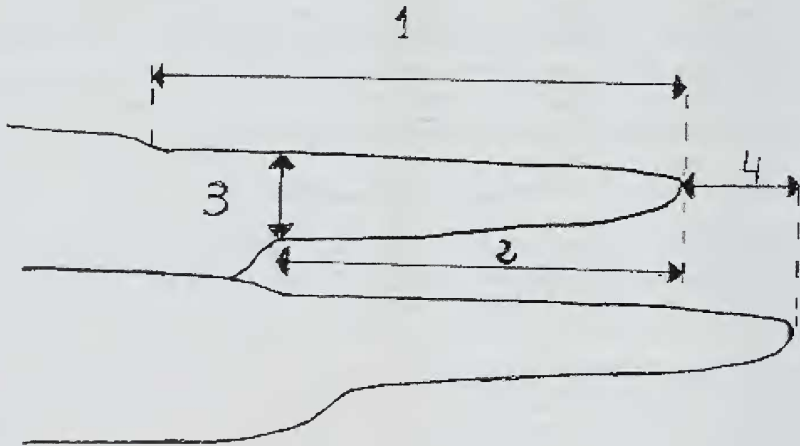

Figure 1. Sketch of primary feathers to indicate measurements taken. Emargination length (1), notch length (2), width of tip (3) and distance between consecutives tips (4)

their wings fully extended; (d) wing width (mm) from the anterior margin at the carpal articulation to the tip of the secondaries with the wing spread; and (e) wing area (cm²) calculated from the outline of the open wing drawn on millimetre-squared paper, and then multiplied by two to give the area of both wings together. We had no access to live male *poecilochrous* and so the wing area was estimated using museum specimens, which were moistened and prepared with their wings fully extended.

Statistical analysis

To seek morphological differences between *polyosoma* and *poecilochrous* we used a stepwise discriminant analysis (Pimentel & Frey 1978). This option gives pooled within-group correlations of variables showing the respective discriminant (canonical) functions. This allows the user to produce a scatter plot of the canonical scores for pairs of discriminant functions (canonical roots) which permits determination of the contribution of each discriminant function to the discrimination between groups. The analysis, using 19 morphometric variables, was applied to four different groups: the males and females of both taxa. Birds were allocated to these categories on the basis of their measurements, without taking into account differences in plumage. The wide range of body measurements used in the analysis allows us to determine objectively which is the most important in separating the four groups. Only 62 birds were used in the analyses, as some were excluded because of missing measurements. The following lengths were used as variables: culmen from the base, tarsus, cubito-radius, wing length, length of P10, notch of P10, emargination and notch of P9 and P8, notch of P7, innermost and outermost secondary lengths, finger width of P10, P9 and P8 (at the point where both emargination and notch coincide) and tail. In graphical presentation, the position of the individual birds is determined by the two most important canonical variables.

The Mahalanobis distance is a classification derived from the discriminate which measures the affinity between elements classified in a multidimensional space. In this case, birds were positioned in accordance with their body measurements. The Mahalanobis distance is measured in terms of standard deviations from the mean of the training samples; the reported matching values give a statistical measure of how well the spectrum of the unknown sample matches (or does not match) the original training spectra. This allows us to measure standard distances between the centroids of a cluster based on the dispersion its components. These distances are similar to the squared Euclidean distances of the respective case from the centroids for each group (the point defined by the means for all variables in the respective group). However, unlike the Euclidean distance, the Mahalanobis distance takes into account the inter-correlations between the variables in the model (which define the multivariate space).

Additionally, pooled data of sexes and taxa were reclassified using a principal components analysis (PCA) (Frey & Pimentel 1978). This analysis allowed us to evaluate the extent to which different body measurements were associated with sex and taxa. We used 18 body measurements: culmen from base, tarsus, cubito-radio,

wing length, length of P10, the distance between the tips of the primaries P10-P9, P9-P8, P8-P7, P7-P6, notches P10, P9, P8, emarginations P9, P8 and P7, outermost secondary length, width of tip P9 and P10. N = 50; birds with missing data were excluded. Briefly, the PCA generates new variables (principal components), based on correlations among the original variables (body measurements), and identifies each individual bird in relation to them. The interpretation of the principal components relies on the factor loadings of the original variables, which are the correlations between the respective variables and components. If there is any consistent pattern of variation associated with sex in both species, this will show up in a plot of the individual scores on the principal components.

The non-parametric Mann-Whitney test (Siegel 1956) was used for independent samples to discover whether differences existed between the two species in wing projection or in the fraction in which the primaries surpass the secondaries in the total wing length when folded. Twenty birds of each species were used without distinction in sex or age.

Another discriminant analysis was used to test whether *polyosoma* and *poecilochrous* maintain the same morphological differences when they coexist at high altitudes in the same region, as well as to determine whether *polyosoma* exhibits geographical variations. The analysis was applied to migrant female *polyosoma* from the Altiplano, to female *polyosoma* from the extreme south of their range, and to female *poecilochrous* from the Altiplano. We were unable to carry out this analysis for males due to the small sample size for *poecilochrous* males from the Altiplano. In this analysis we used the following variables: culmen from base, culmen from cere, cubito-radius, wing length, alula, emargination and notch of P9 and P8, emargination of P7, inner and outer secondary length and basal width of the finger of P9.

Results

Morphometrics
The stepwise discriminant analysis (males and females of each taxon) showed that each of the four groups is separable from the others (Fig. 2), (ANOVA, F30,109 = 14.30, p<0.001). The length of the outermost secondary, culmen from base, wing length, cubito-radius, notch of P10 and P8 are the body measurements which contributed significantly in the discriminant function.

Males and females of the same species were more similar than the same sexes of distinct species. The Mahalanobis distance showed that the sexes of each species resemble each other more than they resemble other clusters: between sexes for *B. polyosoma* the distance is 23.6 and for *B. poecilochrous* 34.1; *B. polyosoma* females differ by 46.6 from *B. poecilochrous* males and by 80.3 from *B. poecilochrous* females, while *B. polyosoma* males differ from *B. poecilochrous* males by 83.8.

Based on morphology, multivariate factorial principal components analysis showed four well-defined and separate groups of birds (Fig. 3). Each group
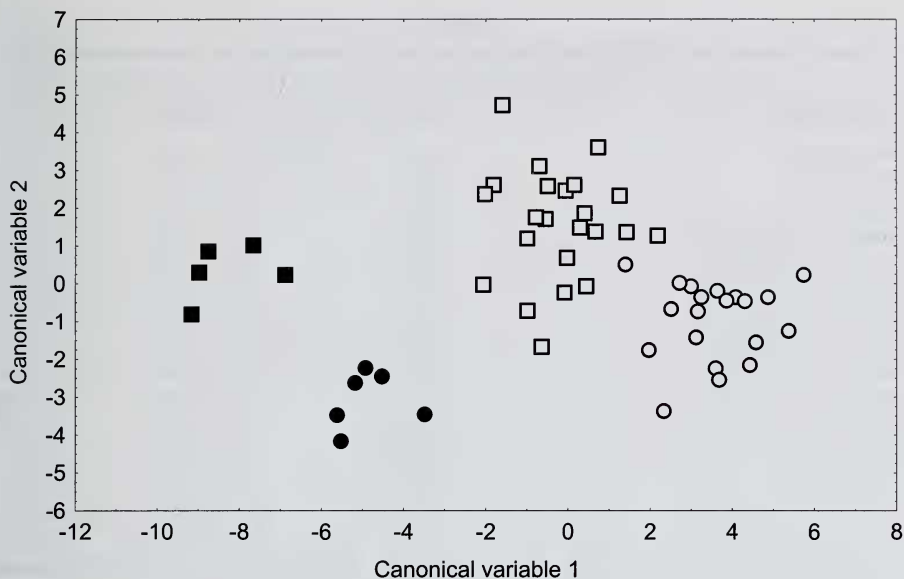
Figure 2. Stepwise discriminant analysis based on 19 morphometric measurements of *B. polyosoma*, males, (○) and females (□), and *B. poecilochrous* males, (●) and females (■). N = 62.
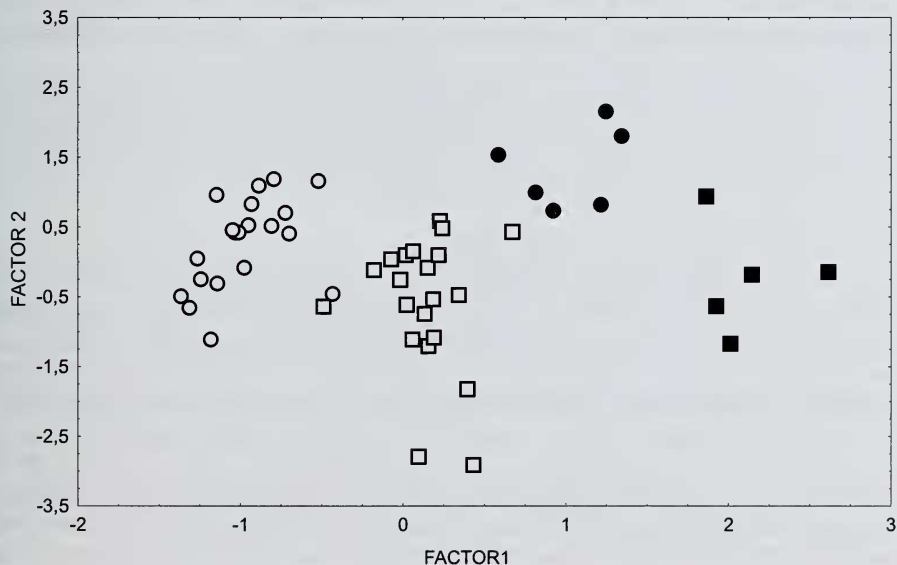

Figure 3. Clusters established by means of a principal components analysis based on 18 morphometric measurements, N = 51. Symbols as Fig. 2.

TABLE 1

Measurements used in the principal components analysis with significant factor loadings (p < 0.07).

Measurements	Factor 1	Factor 2
Cubito-radius	0.86*	-2.53
Wing length	0.95*	-1.18
Length P10	0.89*	0.11
Distance from P10 to P9	0.70*	-0.15
Distance from P9 to P8	0.37	0.78*
Inner notch length P10	0.86*	0.13
Emargination length P9	0.93*	-0.02
Inner notch length P9	0.91*	0.11
Emargination length P8	0.89*	-0.07
Inner notch length P8	0.91*	-0.04
Emargination length P7	0.86*	0.02
Width tip P9	0.83*	0.23
Width tip P8	0.85*	0.13

corresponds to one sex of the two taxa under study. Females generally showed negative values with regard to factor 2 and occupied lower positions than males which, on the other hand, tended to show positive values on the same axis. The sexes of each species formed clearly separated clusters; the most influential measurements are shown in Table 1. Average values and the ranges of measurements show that *B. poecilochrous* is bigger than *B. polyosoma*, with significant differences in most parameters, both between taxa and sexes (Table 2).

B. poecilochrous males are slightly larger than *B. polyosoma* females, although there is extensive overlap of values. Wing lengths of birds of the same sex do not overlap in different taxa (Fig. 4). Neither male nor female *B. polyosoma* ever possess the wingspan or wing width of *B. poecilochrous*.

Wing shape, silhouette and wing loading
In relation to wing span and tail length *B. polyosoma* has a somewhat narrower wing than *B. poecilochrous* (Table 3). It also has longer wings compared to wing width, the alula and the outermost primary. Compared to *B. polyosoma*, *B. poecilochrous* has a proportionately longer distance from the base of the humerus to the carpal joint and a shorter distance from the base of the humerus to the wing tip, according to the ratios of wingspan and the length of the cubito-radius to wing length.

Compared to the maximum length of the outspread wing, the wing of *B. poecilochrous* is 17% wider than in *B. polyosoma*. This percentage was obtained from the outline drawing of the wings of live birds. *B. polyosoma* has greater wing projection than *B. poecilochrous* (Mann-Whitney test Z = 3.97, p<0.001). In the former, the primaries surpass the secondaries in the folded wing by 33.7%, when compared to the total wing length, while in the latter the value is 39.8%. De Vries

TABLE 2

Means and range of measurements of *B. polyosoma* and *B. poecilochrous* males and females. Mass (g), lengths (mm) and surface area (cm^2). Levels of significance * = p<0.01 and ** p<0,001 (ANOVA) are shown between species (column A), sexes (column B) and interaction (column C)

| | | *B. polyosoma* | | | | | | *B. poecilochrous* | | | | | | | |
| | Males | | | Females | | | Males | | | Females | | | | | |
	N	x̄	Range	N	x̄	Range	N	x̄	Range	N	x̄	Range	A	B	C
Mass	16	695,5	(501 – 822)	4	880	(790 – 980)	8	840	(700 - 950)	12	1168	(1010 - 1280)	**	**	*
Culmen	31	21,9	(19,9 - 23,6)	31	24,4	(22,2 - 27,9)	10	22,8	(19,9 - 25,3)	12	25,4	(23,1 - 27,5)	**	**	—
Culmen from base	32	32,9	(29,8 - 36,1)	36	36,4	(33,4 - 39,7)	14	34,5	(32,1 - 37,9)	13	38,1	(35,7 - 40,3)	**	**	—
Cranial width	27	45,9	(42,3 - 55,3)	27	49,2	(44,6 - 52,3)	7	47,9	(44,7 - 50)	10	49,4	(46,5 - 50,9)	—	**	—
Tarsus	35	85,2	(78,8 - 96,9)	41	90,3	(80,0 - 102,1)	17	92,2	(86,4 - 103,7)	23	96,8	(89,1 - 109)	**	**	—
Inner toe	33	18,7	(15,2 - 23,4)	31	19,6	(16,7 - 21,8)	16	20,3	(19,1 - 22,1)	17	22,2	(19,6 - 25,5)	**	**	—
Middle toe	33	29,7	(25,5 - 33,6)	31	32,1	(25,4 - 36,3)	16	33,5	(31,7 - 35,1)	17	36,2	(33,7 - 38,7)	**	**	—
Outer toe	33	21,2	(17,4 - 24,9)	31	23,4	(20,3 - 26)	16	23,6	(21,3 - 26,5)	16	25,4	(24,1 - 27,1)	**	**	—
Hind toe	34	21,1	(17,9 - 23,7)	31	22,9	(20,4 - 25,8)	16	23,6	(21,4 - 25,9)	17	25,3	(22,8 - 27,4)	—	**	—
Inner claw	28	22,1	(20,7 - 23,5)	30	24,5	(20,7 - 28,9)	15	24,7	(22,5 - 27,5)	16	27,3	(25,3 - 29)	**	**	—
Middle claw	26	18,7	(17,4 - 20,3)	29	20,9	(18,8 - 24,1)	15	20,6	(17,9 - 22,6)	15	22,2	(20,7 - 23,4)	**	**	—
Outer claw	25	14,8	(13,8 - 16,2)	27	16,2	(13,9 - 18,2)	15	16,5	(14,5 - 17,8)	16	18	(16,7 - 19,3)	**	**	—
Hind claw	25	22,6	(20,1 - 24,3)	24	25,9	(23,3 - 29,8)	14	24,8	(22,4 - 27)	17	27,8	(25,4 - 29,3)	**	**	—
Wing span	8	1126	(1050 – 1150)	3	1213	(1180 – 1260)	2	1307	(1305 - 1310)	7	1474	(1390 - 1490)	**	**	—
Wing length	36	370,2	(342 – 386)	41	406,8	(387 – 446)	17	425,4	(402 - 444)	23	464,3	(450 – 490)	**	**	—
Wing width	7	227,5	(215 – 235)	2	252,5	(250 – 255)	2	272	(270 - 275)	5	309	(305 – 310)	**	**	—
Cubito-radius	33	120	(109 - 128,5)	36	135,7	(121,4 - 149)	13	137,2	(130 - 143,5)	16	146,3	(136,3 - 156)	**	**	*
Alula	34	98,9	(85 – 113)	41	108,5	(98 - 119)	15	117,9	(104 - 126)	22	125,5	(118 - 136)	**	**	—
Length P10	32	173,4	(157 – 192)	40	191,5	(178 – 211)	17	205,4	(183 - 231)	20	219,3	(205 – 232)	**	**	—
Notch P10	34	78,2	(70 – 87)	39	88	(76 - 101)	17	92,7	(81 - 107)	20	101,1	(92 - 117)	**	**	—
Emargination P9	33	154	(140 – 167)	39	166,6	(132 – 193)	17	176,9	(165 - 192)	22	188,9	(179 - 207)	**	**	—
Notch P9	33	92,4	(84 – 106)	39	101,9	(92 – 120)	17	109,3	(96 - 122)	22	118,9	(109 - 131)	**	**	—
Emargination P8	33	130,5	(115 – 147)	39	140,2	(126 – 160)	17	147,9	(134 - 159)	22	160,7	(153 - 170)	**	**	—
Notch P8	33	92,9	(82 – 105)	38	101,5	(91 – 118)	17	112,1	(104 - 125)	21	119,3	(112 - 126)	**	**	—
Emargination P7	33	100	(90 – 113)	38	107,7	(93 – 132)	15	116,5	(100 - 128)	21	130,9	(119 - 142)	**	**	—
Inner Secondary	35	186,4	(154 – 203)	40	205,8	(186 – 231)	17	233	(215 - 248)	23	250,4	(222 - 273)	**	**	—
Outer Secondary	34	155,4	(128 – 174)	40	162,8	(140 – 192)	17	197,4	(182 - 225)	23	204,2	(180 - 229)	**	**	—
Width tip P10	31	18	(13,5 – 21)	39	19,4	(17 – 22)	15	21,6	(19,5 - 24)	18	23,9	(21 - 27)	**	**	—
Width tip P9	31	20,2	(17 - 22,5)	39	22,1	(19 – 26)	14	24,4	(23 - 26)	20	26,4	(23 - 29)	**	**	—
Width tip P8	30	21,2	(18 – 24)	36	23,4	(19,5 – 27)	14	26,2	(24 - 28)	19	28,8	(23 - 32)	**	**	—
P10-P9	32	71,3	(62 – 90)	39	74,8	(65 – 88)	17	77,2	(67 - 85)	18	85,7	(79 - 97)	**	**	*
P9-P8	32	28,9	(21 – 37)	39	31,8	(22 – 47)	16	35	(26 - 58)	20	38,7	(29 - 47)	**	**	—
P8-P7	32	1,9	(-7 – 10)	35	1,9	(-8 – 11)	14	4,6	(-6 - 11)	21	7	(-3 - 19)	**	—	—
P7-P6	31	-13,5	(-30 – 21)	37	-16,1	(-32 – 5)	14	-4,7	(-10 - 3)	17	-6,8	(-17 - -1)	**	—	—
Tail	35	188,4	(168 – 223)	41	209,5	(176 – 240)	17	215,9	(190 - 238)	23	238,9	(215 - 276)	**	**	—
Wing area	6	2097	1972 - 2171	2	2448	2440 - 2454	2	2689	2667 - 2710	5	3431	3263 – 3533	**	**	*

(1973) also noted this fact when applied to wing depth, i.e. the distance from the tip of the innermost primary to the tip of the longest primary, in proportion to wing length.

The outline of the wing tip is more rounded in *B. poecilochrous* than in *B. polyosoma* (Fig. 5), the outermost primary P10 being relatively long and the rest of the outermost primary tips more equal in length (especially P6 and P7). All this produces a rather wide wing shape with a shorter and blunter wing tip. Furthermore, the alula is somewhat longer in *B. poecilochrous* than in *B. polyosoma*.
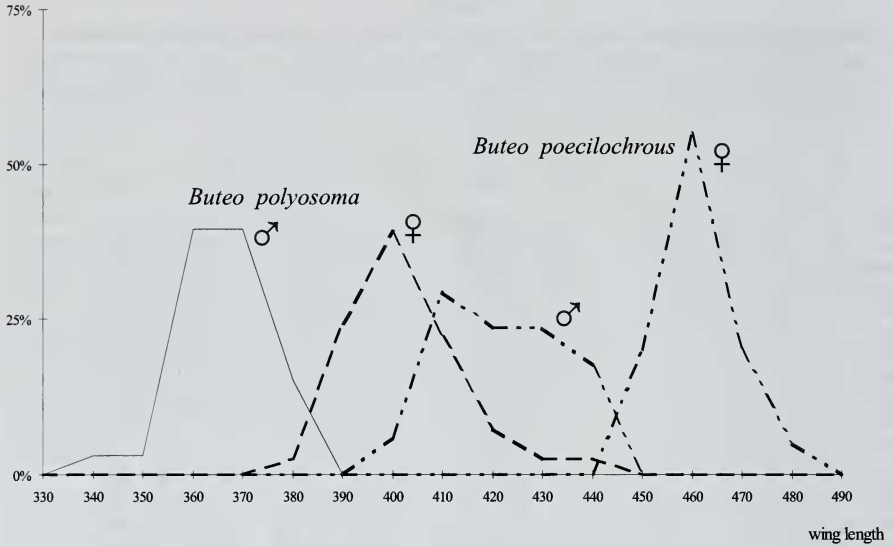
Figure 4. Distribution of wing length (mm) in 118 specimens of *B. polyosoma* and *B. poecilochrous*

Figure 5. From left to right: darker males of *B. polyosoma, B. poecilochrous* and *B. albicaudatus.* Specimens from the collection of the Estación Biológica de Doñana. Photograph by Benjamín Busto.

TABLE 3

Ratios in some wing parameters in male and female *B. polyosoma* and *B. poecilochrous*.
LP10 = length of primary 10.

| | B. polyosoma | | | | | | B. poecilochrous | | | | | |
| | Male | | | Female | | | Male | | | Female | | |
	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.
Wing span / wing width	8	5.06	0.03	2	4.91	0.16	2	4.80	0.07	5	4.40	0.05
Wing length / wing width	8	1.64	0.09	2	1.61	0.01	2	1.56	0.03	5	1.49	0.03
Cubito- radius / wing length	31	0.32	0.11	36	0.33	0.14	13	0.32	0.16	14	0.47	0.10
Wing span / wing length	10	3.00	0.12	3	2.98	0.09	2	3.10	0.01	7	3.20	0.08
LP10 / cubito- radius	33	1.45	0.07	36	1.41	0.08	13	1.49	0.09	14	1.51	0.05
Wing length / LP10	28	2.13	0.84	34	2.13	0.82	17	2.03	0.12	17	2.11	0.69
Wing length / alula	33	3.76	0.24	35	3.75	0.20	15	3.62	0.21	19	3.70	0.14
LP10/ alula	31	1.75	0.14	40	1.76	0.11	15	1.74	0.88	17	1.74	0.08
Wing width / tail	8	1.20	013	2	1.20	0.01	2	1.38	0.05	5	1.31	0.05

TABLE 4

Standard and linearised values of wing loading in *B. polyosoma* and *B. poecilochrous*.
S = Wing area (cm²) ; W = Body mass (g).

| Coefficient | B. polyosoma | | B. poecilochrous | |
	Male	Female	Male	Female
S/W	3.01	2.78	3.20	2.94
$\sqrt{S}/\sqrt[3]{W}$	5.17	5.50	5.50	5.56

The wing in *B poecilochrous* is similar to that of *B. albicaudatus* in width and in the pattern of internal markings, although it differs inasmuch as its innermost primaries are somewhat longer and its outermost primaries are shorter; the opposite is true for *B. albicaudatus* (de Vries, 1973). In relation to wingspan and wing width, the tail of *B. poecilochrous* is proportionally shorter than that of *B. polyosoma*.

B. polyosoma has a larger wing loading than *B. poecilochrous* (Table 4). At equal body mass, male and female *B. polyosoma* have 5% and 5.5% less surface area (both wings) respectively than the same sexes of *B. poecilochrous*. In both taxa males have lower wing loadings than their respective females.

Buteo polyosoma *of the Altiplano*
B. polyosoma occurs above 3,500 m during the austral winter in the high Andean region of Bolivia, sharing its altitudinal range, but not habitat, with *B. poecilochrous* (Cabot 1991). A stepwise discriminant analysis with 12 body measurements was applied to female *B. polyosoma* and *B. poecilochrous* from the central Andean

highlands and to *B. polyosoma* from the extreme south of its range. The two groups of *B. polyosoma* had more in common with each other than with *B. poecilochrous* (Fig. 6). The difference between the groups is significant (ANOVA, $F_{24,22}$= 19.76, p<0.001). The statistically significant body measurements that contributed to the discriminant function were the length of the inner and outermost secondaries, the cubito-radius, the culmen from base measurement, the emargination of P9 and the length of the innermost secondary. The *B. polyosoma* from the Altiplano seemed to be slightly smaller than those from the far south of their range in Chile, in the Rio Negro, Patagonia and Tierra del Fuego in Argentina, and the Falkland Islands (Table 5).

Analysis of Stresemann's criterion
Stresemann (1925) argued that in *B. poecilochrous* the fifth outermost primary (P6) is longer than the third (P8), and that the reverse pertains in *B. polyosoma*.

Our results show that in *B. poecilochrous* differences between the tip distance P6-P7 are similar to the P7-P8 distance (Table 2), and show an average difference of 0.1 mm in males and 0.3 mm in females. A small amount of differential weathering between feathers and/or a minimum of natural difference may explain this disparity, present even in the two wings of the same individual. Of the specimens of *B. poecilochrous* examined in this study, 45.4% of females (n = 11) had P6 (fifth)
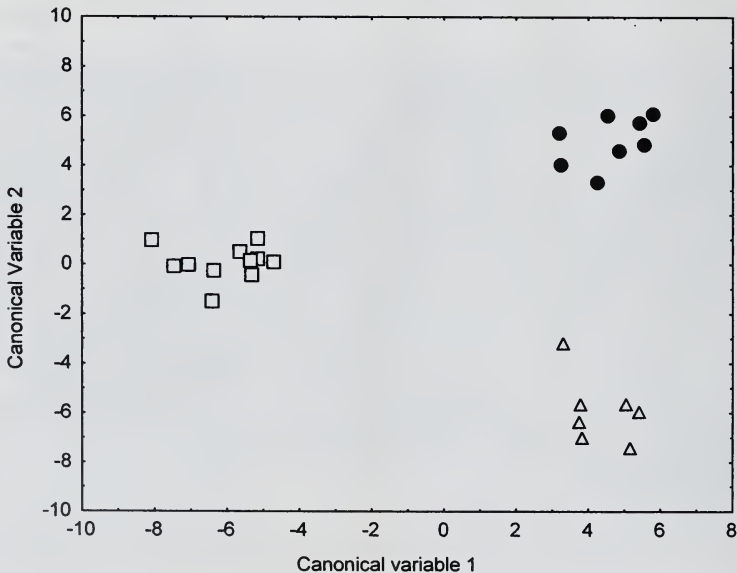

Figure 6. Stepwise discriminant analysis based on 12 morphometric variables from females of *B. polyosoma* from the southern region (△), *B. polyosoma* from the High Central Andes of Bolivia (□), and *B. poecilochrous* from the High Central Andes of Bolivia (●)

TABLE 5

Averages and ranges of measurements (mm) from females of *B. polyosoma* from the Altiplano (n=4) and the southern parts of its range (Patagonia, Tierra del Fuego and Falklands Islands) (n=13).

	Altiplano		Southern Zone	
	$\overline{x}$	Range	$\overline{x}$	Range
Culmen from base	36.5	35.9 – 37	37.1	35.1 - 39.7
Tarsus	85.3	80.0 – 89.6	90.5	83.2 - 99.2
Cubito-radius	130.7	129.0 – 132.0	139.1	132.5 - 145.8
Wing length	395.5	390.0 – 408.0	411.7	392.0 - 446.0
LP10	189.7	186.0 – 196.0	192.3	178.0 - 202.0
Tail	211.3	201.0 – 223.0	218.4	190.0 – 240.0

longer than P8 (third), the same percentage showed the opposite, and 9.1% showed no difference between the feather tips. In males (n = 8) 62.5% had P6 (fifth) longer than P8 (third), 25% the opposite and 12% had both the same length.

In *B. polyosoma* females 92.6% (n = 27) of birds followed Stresemann criterion, 3.7 % (1) did not and the same percentage had both feathers of the same length. The exceptions were due to the growth of P8 being incomplete. All male *B. polyosoma* (n = 22) fulfilled Stresemann's criterion. The average difference between both primaries in *B. polyosoma* was 13.0 mm in males and 16.1mm in females.

Mistakes in the identification of species and sex in museum skins

Errors in sexing
Of the specimens examined, 26.3% (n = 31) had no indication of sex and 7.9% (n = 9) were obviously wrongly labelled: 6.8% (n = 8) of the males were sexed as females, while the remaining 0.8% (n = 1) were females sexed as males. Most of the males sexed as females were *polyosoma*, except for one *poecilochrous*. These specimens are subadults. Birds at this stage show a chestnut-reddish back like the definitive plumage of adult females (Pavez 1998), except for two specimens which had a definitive adult plumage with a grey back.

Errors in identification
Wrongly identified specimens were found in all of the collections studied. A total of 16.7% (n = 7) of all *B. poecilochrous* had been identified as *B. polyosoma*, while only 1.3% (n = 1) of *B. polyosoma* has been identified as *B. poecilochrous*. This high proportion of errors in the determination of *B. poecilochrous* indicates that they had been identified according to Stresemann's criterion or simply misidentified. Other detected mistakes include a *B. polyosoma* identified as a *B. albonotatus*, and two *B. albicaudatus*, one *B. ventralis* and three specimens of *B. albigula* (two of light plumage and one of dark plumage) all identified as *B. polyosoma*.

Discussion

The long debate on the systematics of these taxa has been due to the difficulties experienced by taxonomists when attempting to separate birds in the hand. A series of characteristics exhibited by the species of *Buteo* generate these difficulties. These are: 1) delayed maturation of six years before attaining definitive adult plumage in *B. polyosoma* (Pavez 1998) and *B. poecilochrous* (unpublished data); 2) age-related plumage changes depend on colour phase (Lehmann 1945, Jiménez 1995, Pavez 1998); 3) dimorphic adult plumage (Housse 1945, Vaurie 1962, Pavez 1998); 4) immature males show a chestnut-reddish dorsal patch, as in adult females (Brown & Amadon 1968, Pavez 1998); 5) some plumages appear in both species (Vaurie 1962). *B. polyosoma* and *B. poecilochrous* also share other factors which are common in the genus (Brown & Amadon 1968): two colour morphs (Housse 1945, Lehmann 1945); high individual variability in plumage (Vaurie 1962); medium-size, with some overlapping measurements especially in female *B. polyosoma* and male *B. poecilochrous* (de Vries 1973, Cabot 1991); and overlap in geographical range.

All this leads to a wide array of different plumages with, in addition, interspecific size variations, intraspecific sexual differences and geographical variations in size in *polyosoma* (Jiménez 1995). Variations in shape of specimens, due to differences in preparation, may also have contributed to difficulties in identification.

The unravelling of all these characteristics has been made possible by combining data from museum specimens, captive birds and the field. Previous studies were based on partial and fragmented information extracted from a small (Jiménez 1995), heterogeneous and patchy collection of museum skins which prevented those ornithologists who were not familiar with the species from establishing specific identification criteria. Furthermore, within the examples analysed there are a number of birds belonging to other species, as well as wrongly sexed or misidentified birds (Vaurie 1962, Jiménez 1995 and our results), above all in the cases of *B. poecilochrous* identified as *B. polyosoma*. This last factor is due to the application of the Stresemann rule, a wrongly formulated key which was widely accepted by ornithologists as the only way of separating the species, despite the fact that its effectiveness had been questioned (Hellmayr 1932, Vaurie 1962). This rule gave the species one of the largest ranges of individual size variation among raptors, with very wide ranges given for one sex and very narrow ranges for the other (Brown & Amadon 1968, Blake 1977).

Our statistical analyses of body measurements showed that there are two phenotypes, with differing proportions and sizes, which correspond to *B. polyosoma* and *B. poecilochrous*. They are reasonably easy to separate in flight, and most field observations make no mention of identification problems (Macedo 1964, Fjeldså 1987, Remsen & Traylor 1989, Jiménez & Jaksić 1990, Jiménez & Jaksić 1991, Jaksić *et al.* 1991, 1992).

Between these two taxa, no morphological intergradation related to geographical features has been detected; neither have any field data nor case of morphometry which might suggest hybridisation ever been reported. On the other hand, when *B.*

poecilochrous and *B. polyosoma* share an altitudinal range, sizes and proportions differed.

In *B. polyosoma* body size is linked to geographical features, such that bigger birds occur in the extreme south of the range (de Vries 1973, Jiménez 1995 and our results), smaller birds are found along the coasts of Peru and Ecuador (Swann 1922, Ortíz-Crespo 1986, Fjeldså & Krabbe 1990), while wintering birds in the Altiplano are, on average, slightly smaller than the birds in the southernmost part of the range. In *B. poecilochrous* no size variation was detected according geographic factors.

Farquhar (1998) considered that *B. poecilochrous* is conspecific with *B. polyosoma* based on the following conclusions from the material he examined:

a) wing length and wing formula varied clinally and could not therefore be used to separate the species.
b) in adults and juveniles the shape of the wing tip changed in relation to wing length.
c) wing length varied according to body size and mass, both of which varied with altitude.
d) body colour exhibited huge variation throughout the range.
e) the alarm call given throughout the range did not differ.

Farquhar used incorrect methodology and interpretations:

a) Following Vaurie (1962), Farquhar recognised only two age classes, adults with a white tail and subterminal black band and immatures with a brownish-grey tail with fine dark barring. This classification gives the species a far greater polymorphism than really exists, since it covers the sequential age-related plumage changes which occur as birds attain their definitive adult plumages (Pereyra 1938, Housse 1945, Goodall *et al.* 1951, Jiménez 1995).
b) He failed to attribute variations in colour and plumage patterns to chance and also did not question whether light and dark morphs exist. Likewise, he did not link variation in plumage with sex (Vaurie 1962, Housse 1945, Pavez 1998).
c) He only compared alarm calls, which sometimes resemble those of other *Buteo* species (de Vries 1973). Furthermore, the calls he obtained were from females of four pairs which, surprisingly, correspond to three different silhouette types: long, rounded wing; short, pointed wing and wing long, pointed wing. Fjeldså & Krabbe (1990) noted that calls differ between the two species.
d) He did not analyse available information regarding morphological, ecological and behavioural aspects, which help to separate the two taxa.

As a result of these misinterpretations, Farquhar (1998) obtained a great variety of colour forms with no apparent correlations. He obtained a continuum of wing lengths and shapes which he related, without going into detail, to altitude. In fact, his birds with long wing length (female *B. poecilochrous*) and (smaller) short wing length were at the ends of the continuum, with overlapping male *B. poecilochrous* and female *B. polyosoma* in the middle.

Information available regarding other aspects of the natural history of these birds highlights the differences between the two taxa and agrees with our conclusions. Namely:

a) Plumage morphs. In *B. polyosoma*, pale-morph birds make up almost the whole population, except in Tierra de Fuego and the Falklands Islands where darker birds predominate (Reynolds 1935, Woods 1988). In *B. poecilochrous*, the ratio of dark/pale birds is 50:50, or sometimes with a slight proportion in favour of dark birds (Meyer de Schauensee 1970, de Vries 1973); no geographical variations are documented.

b) Use of space. *B. polyosoma* is a generalist and occurs in a broad variety of regions, while *B. poecilochrous* is restricted to a specific mountainous habitat over 3,500 m (Meyer de Schauensee 1970, Fjeldså 1987, Fjeldså & Krabbe 1990). The two species do not mix where they coexist (Cabot & Serrano 1986, Cabot 1991).

c) Food. *B. polyosoma* takes medium- and small-sized mammals, as well as occasionally larger prey such as domestic fowl, European hares and rabbits (Schlatter *et al.* 1980, Woods 1988, Jiménez & Jaksić 1991). *B. poecilochrous* has a more broad-based diet, both in size and type: earthworms, spiders, beetles, wasps, grasshoppers, fish, frogs' eggs, frog larvae, lizards, birds' eggs, birds, small- and medium-sized mammals such as Cottontails *Sylvilagus* (Lehmann 1945, Macedo 1964, Solís & Black 1985, Jimenez & Jaksić 1990).

d) Hunting techniques and eco-morphology. *B. polyosoma* hunts from look-out points (Bellati 2000) or from low over the terrain (Rocha & Quiroga 1996). *B. polyosoma* has a shorter wingspan, greater wing loading and narrower and more pointed wings which give it, therefore, greater propulsion for flapping flight and more speed and inertia when gliding. A proportionally longer tail also confers greater manoeuvrability. *B. poecilochrous* hunts from the air at considerable height (Rocha & Quiroga 1996), sometimes hunting co-operatively (Cabot 1988), and also walks in search of invertebrates (De Vries & Coello unpublished.). *B. poecilochrous* has the typical features of a glider, with a large wingspan, broad wings, wings with long slots, a large alula and a lower wing loading. These permit high manoeuvrability at low speed, great soaring capabilities, static uplift (Welty 1982) and greater capacity to hang and hover. It holds its wings elevated in a V-form and the broad, short tail permits static climbing in close spirals.

e) Movements. The *B. polyosoma* populations in Patagonia and Tierra del Fuego winter in lowland areas of central and northern Argentina and neighbouring countries. Birds wintering in the Altiplano are thought to originate from central and western Argentina and central Chile, where numbers fall in winter (Jiménez 1995). In *B. poecilochrous* only altitudinal movements to lower areas around 2,000 m in winter in the extreme south of its distribution have been recorded (Jaksić *et al.* 1991).

f) Breeding behaviour. *B. polyosoma* is monogamous and no cases of polyandry have ever been recorded in its extensive range. In *B. poecilochrous*, 75% of

breeding birds at Antisana Mountain in Ecuador are polyandrous (Solís & Black 1981, De Vries & Coello unpublished)

All the above indicate that *B. polyosoma* and *B. poecilochrous* should be treated as different taxa. Selective processes have led to mechanisms of ecological speciation. These include the diversification of all aspects of the phenotype, including the evolution of differences that allow the exploitation of different ecological resources, and thus permit coexistence in sympatry. We conclude, therefore, that, according to the biological species concept, *B. polyosoma* and *B. poecilochrous* are isolated species and that their respective specific statuses must be conserved.

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The correct publication date of *Aplonis corvina* (Kittlitz, 1833)

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The recent paper by Hume (2002) contains both an error and confusion regarding the publication details of the name *Aplonis corvina*. The error is that the name should have been written as *Aplonis corvina* (Kittlitz, 1833), because the species was originally described by Kittlitz as *Lampothornis corvina.* The confusion relates to the dating: Hume (2002) followed Amadon (1962) in giving the date of publication as 1833, but then referenced the relevant work (the second part of Kittlitz's *Kupfertafeln zur Naturgeschichte der Vogel* - hereafter *Kupfer. Nat. Vog.*) as 1832, a date that has also been used by some authors.

The Rothschild Library at The Natural History Museum, Tring, has a bound copy of the three published parts (= Hefts) of *Kupfer. Nat. Vog.*, each preceded by its original title page. The title page of the first part is dated 1832, whereas the second and third parts are both dated 1833. The correct publication date for *Aplonis corvina* and other taxa described in the second part is thus 1833. In its entirety, *Kupfer. Nat. Vog.* should be referenced as Kittlitz (1832-33).

A further potential source of confusion, avoided by Hume (2002) but for completeness worth mentioning here, is that Kittlitz (1835) also published a more detailed description and illustration of *A. corvina* in volume 2 of the *Memoirs of the Academy of Imperial Sciences, St. Petersburg,* the title page of which is imprinted 23 November 1831. However, this "1831" paper in fact was not published until 1835 (imprinted title page of the memoirs) and so does not constitute the type description, despite being referenced by Kittlitz (1833) and clearly intended by him to appear first.

For information concerning the nomenclature of *A. corvina* and other nomenclatural matters, the following website, set up by A. Peterson, is available online: http://www.zoonomen.net/